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MIDDLE DEVONIAN FORAMINIFERA FROM THE HOLY CROSS MOUNTAINS (POLAND)

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Abstract: The Middle Devonian was an exceptional time for foraminiferal evolution because of the emergence of the first true calcareous multilocular taxa. Despite being key forms for an understanding of the origin of foraminiferal multilocularity, which is one of the most intriguing events in the evolutionary history of the group, they are largely unstudied. These unique foraminifera, including representatives of the genera *Cremsia*, *Moravammina*, *Pseudopalmula*, *Semitextularia,* and *Vasicekia,* are presented herein as well as foraminifer-like microfossils of uncertain biological position. The studied material comes from the Middle Givetian strata of the Miłoszów section and the Eifelian part of the Grzegorzowice-Skały section (Holy Cross Mountains, Poland). Described isolated specimens are in an exceptionally good state of preservation on a worldwide scale, which enabled the detailed analysis of test morphologies, complementing previous papers based on less well-preserved material. The suggested systematics of the foraminifera collected attempts to revise scarce taxonomic data that is still under debate, especially the classification of *Moravammina*, *Cremsia,* and *Vasicekia*. The Devonian foraminifers presented were prominent endobenthic and epibenthic inhabitants of common organic coral-stromatoporoid buildups. Palaeobiogeographical records show that during the Middle Devonian, the studied forms extended their exclusive European distribution into further Laurussian shelves and shallow seas, located in the northern and southeastern parts of the Rheic basin. This assumes that such assemblages may be used as palaeoenvironmental indicators. However, at present, their correlative potential is unknown.

Key words: Foraminifera, Devonian, systematics, palaeobiogeography.

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INTRODUCTION

The Foraminifera originated in the Neoproterozoic as non-shelled descendants of cercozoans, according to molecular clock data (Pawlowski *et al.*, 2003), but these early Foraminifera left no fossil record. Therefore, the early history of the Foraminifera is poorly known. The first foraminifers with mineralized tests were found in the Lower Cambrian (Ross and Ross, 1991; McIlroy *et al.,* 1994, 2001; Cope and McIlroy, 1998; Vachard *et al*., 2010), thus the ability to produce a mineralized test most likely developed during the Cambrian biotic explosion. In the Cambrian, the Foraminifera were a rare and undiversified group, represented mostly by a community of organic-shelled unilocular monothalamids, extremely simple, tubular and spherical agglutinated forms (McIlroy *et al.,* 1994, 2001; Cope and McIlroy, 1998) or characteristic for the Cambrian, spiral bilocular *Ammodiscus*, *Glomospira*, and *Turritellella*, composed of organic or agglutinated shells (Culver, 1991, 1994; Culver *et al.,* 1996; Kaminski *et al.,* 2009). The first pseudo-multichambered forms most likely appeared during the early Middle Ordovician (Kaminski *et al.,* 2008, 2010). These were agglutinated and morphologically simple (tubular, elongated uniserial or vase-shaped), and belonged to several genera, such as *Lakites, Amphitremoida, Lavella, Ordovicina, Pelosina, Reophax*, *Hyperammina*, and *Saccamminida* (Gutschick, 1986; Nestell *et al.,* 2009). More recently, an agglutinated assemblage, containing uniserial pseudo-multichambered and chambered forms, including *Subreophax*, *Reophax*, and *Hormosina*, has been documented from the middle upper Ordovician (Katian) of Central Saudi Arabia (Kaminski *et al.*, 2019). The earliest agglutinated multilocular Foraminifera (*Ammobaculites* and *Sculptobaculites*) made their first appearance in the middle part of the Early Silurian (Aeronian) in Saudi Arabia (Kaminski and Perdana, 2017, 2020).

The first calcareous foraminifers, which were single-chambered forms, possibly appeared during the Late Silurian (Ross and Ross, 1991; Vachard *et al.,* 2010). However, the stratigraphic position of the event is still under debate. *Saccamminopsis*, commonly regarded as the first calcareous form, first described as coming from the Late Ordovician, turned out to be Devonian after a later investigation (Scott *et al.,* 2003).

Such a morphologically simple foraminiferal community occurred up to the Middle Devonian, until the emergence of calcareous multilocular forms with true chambers, such as the bilocular flat and fan-shaped Semitextulariidae or planispiral and trochospiral Nanicellidae (Vachard *et al*., 1994; Vachard, 2016; Dubicka, 2017) during the so-called "Givetian Revolution" (Vachard *et al.,* 2010). This radiation is claimed to be one of the most significant events in the entire history of the group and was most probably linked with the evolutionary development of the main modern foraminiferal clades (Pawlowski *et al.,* 2003, 2013; Dubicka and Gorzelak, 2017) and of some groups of foraminifera that died out completely (Dubicka *et al.,* 2021a). This Devonian radiation might have been related to the emergence of foraminiferal symbiosis (kleptoplasty) with microalgae, which enabled foraminifera to remain photosynthetically active and largely benefit from the photosynthetic process (Dubicka *et al.,* 2021b). Devonian multichambered foraminifera settled carbonate platforms that developed in shallow, warm, environments with high calcium carbonate production, including unique stromatoporoid-coral buildups (Racki and Soboń-Podgórska, 1993; Vachard *et al.,* 2010). The strong connection between Foraminifera and their environment is confirmed by their joint disappearance during the Frasnian/Famennian biotic crisis (Ross and Ross, 1991; Vachard *et al.,* 2010; Dubicka, 2017). Despite the fact that Eifelian–Givetian time was one of the most crucial periods for foraminiferal evolution (Pawlowski *et al.,* 2003; Vachard *et al.,* 2010), with the development of the first complex multichambered calcareous forms, Middle Devonian foraminiferal communities are still poorly known. A few studies were carried out mainly in the 1950s with the usage of thin sections that enabled detailed morphological and structural analysis. This paper is an attempt to shed new light on the taxonomy, ecology, and distribution patterns of Devonian foraminifera, on the basis of studies of rich assemblages from the Skały Formation, cropping out at Miłoszów and Skały (Holy Cross Mountains, Poland).

MATERIAL AND METHODS

The microfossils in the present study were extracted from Middle Devonian strata of the northern region of the Holy Cross Mountains (Szulczewski, 1995), Upper Eifelian to Middle Givetian in age. In terms of lithostratigraphy, the studied strata belong to the Skały Formation (Racki *et al*., 2022). The outcrops are located within the Grzegorzowice-Skały succession (Pajchlowa, 1957; see also Halamski, 2022, fig. 1C), although at some distance from the Dobruchna valley, and at Miłoszów (Halamski, 2022, fig. 1B; Halamski *et al.*, 2022).

Seven samples were taken from the Skały section (Fig. 1). They all belong to the lower part of the Skały Formation and are Late Eifelian in age. As discussed in detail by Racki *et al.* (2022), the precise stratigraphic position of these samples taken from a temporary outcrop situated eastwards from the main section, is not entirely certain. They were initially identified with brachiopod shales (Dobruchna Member *sensu* Racki *et al.*, 2022; set XIV *sensu* Pajchlowa, 1957), but rather might represent the overlying set XV. It should, however, be stressed, that the genuine "brachiopod shales" (set XIV), do contain Devonian Foraminifera (Duszyńska, 1956; see also Halamski and Zapalski, 2006; Woźniak *et al*., 2022). The Dobruchna Member is well constrained stratigraphically and is Late Eifelian in age (Dzik, 1981; Malec and Turnau, 1997; Halamski, 2005; Racki *et al.*, 2022).

Also, seven samples were collected from section M-0 at Miłoszów, more precisely from beds 4, 5, 7–10; these beds belong to the Middle Givetian (the approximate equivalent of set XXVA at Skały; Halamski *et al.*, 2022). Five samples were taken from the shales, belonging to the Lower Givetian section M-1 at Miłoszów (M1-IIa).

Mechanically disintegrated marly rock samples from the studied sections were treated, following the standard maceration technique with Glauber salt (Witwicka *et al.,* 1958) and Rewoquat (Jarochowska *et al*., 2013). After cleaning in an ultrasonic cleaner, the residue was sieved through sieves with a mesh size of 0.053 mm and dried in a laboratory drier. Isolated specimens of foraminifera and microfossils of uncertain biological affinity were manually collected from the residuum and analyzed under both a stereoscopic (NIKON SMZ 18) and a Zeiss Σigma VP field-emission scanning electron microscope, at the Faculty of Geology, University of Warsaw. The systematic interpretations and photographic documentation were also conducted with the usage of the latter microscope.

Some selected isolated specimens were additionally used for the preparation of five thin-sections slides containing 30 specimens each. Foraminifera were embedded in glue and then polished in the laboratory of sample preparation at the Faculty of Geology, University of Warsaw, Poland. Thin sections enabled insight into the internal structure of all studied forms that allowed making a detailed description of the arrangement of their chamberlets. Slides were subsequently analyzed and photographed under the stereoscopic microscope at the Faculty of Geology, University of Warsaw, Poland.

When possible, 100 specimens of all calcareous microfossils were picked randomly from each sample. To obtain general information about the diversity and variability of the studied microfossil community, the material was subjected to qualitative and quantitative analysis. Details about the number of counted specimens of each taxon per sample are presented in Figure 1.

All microfossil material collected was deposited in the S. J. Thugutt Geological Museum (Faculty of Geology, University of Warsaw, Poland).

RESULTS

Eleven different morphological forms of calcareous microfossils were obtained from Miłoszów and Skały, including Foraminifera and some fossils of uncertain systematic affinity but resembling Foraminifera. Six of them undoubtedly can be classified as Foraminifera with clearly visible

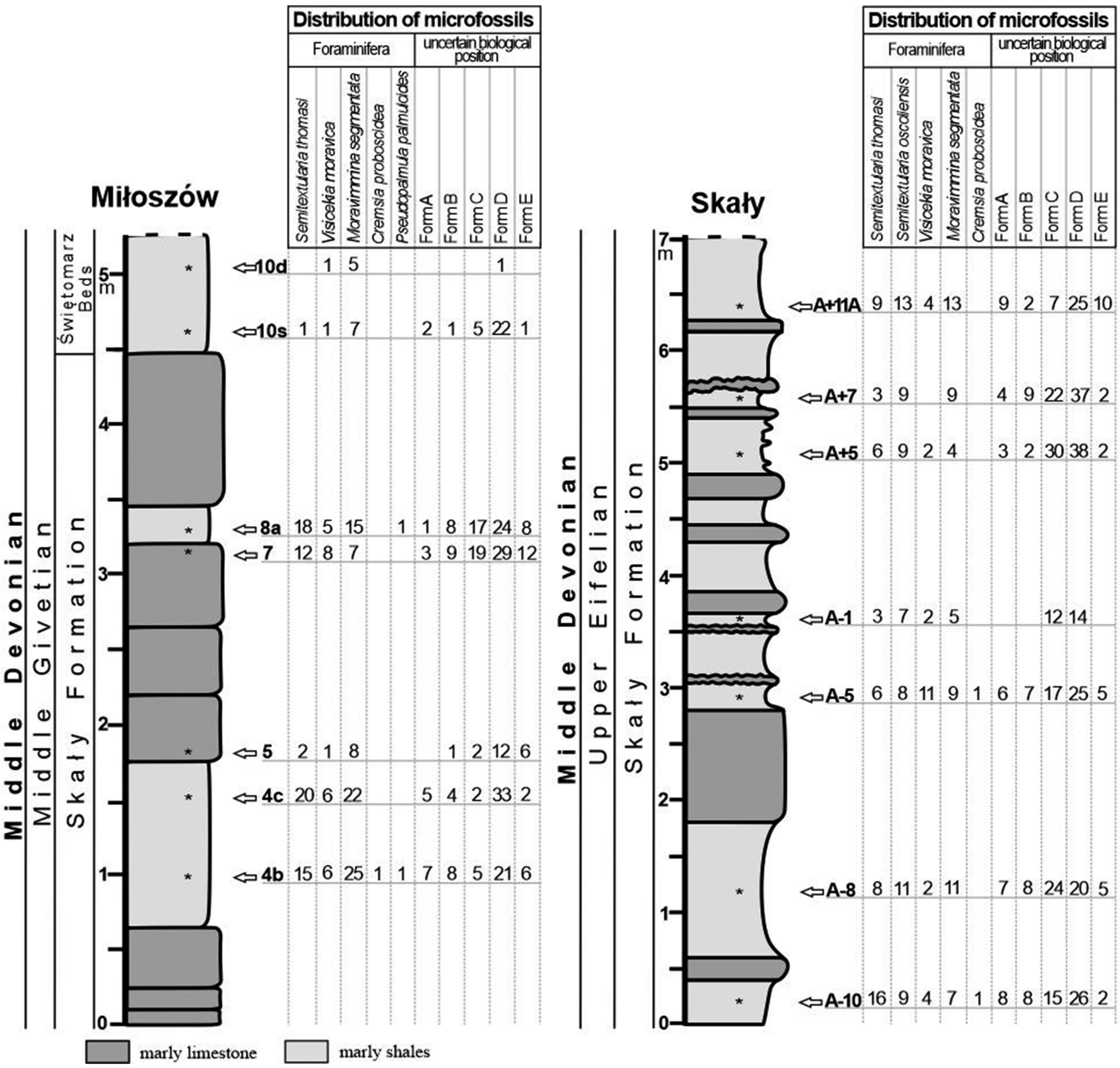

Fig. 1. Generalized lithology and stratigraphy (after Racki *et al.,* 2022 and Pisarzowska *et al.,* 2022) of Miłoszów and Skały sections with the distribution of the studied Foraminifera and microfossils of questionable biological affinity.

chamber compartments and proloculi. They belong to five genera: *Cremsia, Semitextularia*, *Moravammina*, *Vasicekia,* and *Pseudopalmula*. The other forms do not display clear foraminiferal features; these have been left in open nomenclature and named Forms A–E. For detailed descriptions and distribution patterns of all distinguished taxa see the taxonomic notes and Figures 1–4.

Miłoszów section

Four representatives of true Foraminifera and five foraminifera-like forms (A–E forms) were recorded in all analyzed samples (4b, 4c, 5, 7, 8a, 10s, 10d) from the Miłoszów sections (Fig. 1). However, all the studied taxa were collected from only two samples (4b and 8a). Only scarce specimens, mostly their fragments, were found in samples 5, 10s, and 10d, of which sample 10d was the most poorly represented.

The most frequently recorded Foraminifera were *Semitextularia thomasi* specimens, accounting for up to 20%, while moravamminids comprise up to a quarter of all microfossils in the studied assemblages. *Vasiceikia moravica* was recorded in all Miłoszów samples but amounts to less than 10%. Only a few specimens of *Cremsia proboscidea* were present in samples 4b and 8a, while *Pseudopalmula palmupuloides* occurred exclusively in sample 4b.

Foraminifera-like forms (A–E) were present in all studied samples, in significant amounts of up to 70% of the entire assemblage of sample 7. Tubular Form D generally occurred most abundantly, which in the case of sample 4c accounted for almost half of all collected specimens. Probable bryozoan remains (forms A–C) occurred in the vast majority of studied samples but were most abundant in samples 7 and 8a, dominated by the massive Form C. Genuine bryozoans are numerous at Miłoszów (Halamski *et al.*, 2022; Pisarzowska *et al.*, 2022).

Skały section

In samples from the Skały section, two *Semitextularia* species were found; *S. oscolinensis* was more common than *S. thomasi*, except in sample A-10. *Moravammina segmentata* and *Vasicekia moravica* each comprised up to 13% of all collected specimens. The least frequently occurring foraminifera was *Cremsia proboscidea*, singular tests of which were found in two samples, A-5 and A-10. Foraminiferal representatives constituted from about 20% of microfossil assemblage in sample A+5 to 40% in sample A+11. The vast majority, nearly 80% of the collected specimens in the samples studied, were foraminifera-like forms (A–E), among which tubular Form D occurred most abundantly. Massive Form C was also frequent, especially in samples A+5 and A-8. Despite being absent in the very poorly represented sample A-1, forms A, B, and E constituted a similar number of specimens, each reaching from 2 to 10 per sample.

SYSTEMATIC PALAEONTOLOGY

The systematics of the studied Devonian foraminifera used herein follows the classification of Vachard (2016).

Foraminifera
Phylum Foraminifera (d'Orbigny, 1826)
Class Fusulinata Gaillot and Vachard, 2007
Order Pseudopalmulida Mikhalevich, 1993
Family Semitextulariidae Pokorný, 1956
Genus Semitextularia Miller and Carmer, 1933
Semitextularia thomasi Miller and Carmer, 1933
Fig. 2A–G, O–R

1933 *Semitextularia thomasi* – Miller and Carmer, p. 428, pl. 50, fig. 10a–e.

1943 *Semitextularia thomasi* Miller and Carmer – Cushman and Stainbrook, p. 77, pl. 13, figs 24–28.

1951 *Semitextularia thomasi* Miller and Carmer – Pokorný, pp. 19–20, fig. 15.

1955 *Semitextularia thomasi* Miller and Carmer – Bykova, pp. 52–53, pl. 18, figs 9–11.

1955 *Semiextularia thomasi* Miller and Carmer – Copeland and Kesling, pp. 105–112, pl. 1.

1956 *Semitextularia thomasi* Miller and Carmer – Duszyńska, pp. 25–30, pl. 1.

1959 *Semitextularia thomasi* Miller and Carmer – Duszyńska, pp. 78–81, pl. 2.

1965 *Semitextularia thomasi* Miller and Carmer – Chuvashov, pl. 14, fig. 11.

1966 *Semitextularia* sp. – Mouravieff and Bultynck, p. 154, pl. 1, figs 1–7.

1966 *Semitextularia thomasi* Miller and Carmer – Sobat, pp. 237–243, pl. 23.

1975 *Semitextularia* sp. *thomasi* Miller and Carmer – Kettenbrink and Toomey pl. 2, fig. 1.

1982 *Semitextularia* sp. – Mamet and Plafker, p. 4.

1993 *Semitextularia thomasi* Miller wand Carmer – Racki and Soboń-Podgórska, p. 274, fig. 13b, c.

2011 *Semitextularia thomasi* Miller and Carmer – Fijałkowska-Mader and Malec, p. 129.

2019 *Semitextularia* sp. – Nazarova *et al*., pl. 5, fig. 4.

Material: More than 150 well-preserved specimens.
Description: The test is free, flattened on both sides, and somewhat fan-shaped with an irregular outline, caused by the variable curvature and elongation of the chambers. The number of chambers is also variable both in uniserial (from 6 to10) and biserial parts of the test (up to 8 chambers). Usually, the arrangement of the first few earliest chambers is not clearly visible. Early chambers are rather short, semiovate, and biserially arranged. Chambers of the uniserial part are narrow, variably U-arched, and horizontally elongated. Sutures between chambers are narrow, shallowly depressed, and less distinct in the biserial part. Test walls are imperforate and composed of calcite. Test microstructure is compact and lamellar. Some ornamentation in form of mesoporous structure with triangular pinholes is visible on the surface of well-preserved specimens. Chambers are subdivided into so-called chamberlets, which are slightly marked on the test surface by separated thick rib-shaped pillars. In cross-sectional view, chamberlets are presented as small ovate holes, located distinctively and lined up alongside the chamber width. The multiple apertures at the top of the last chamber consist of small holes arranged in a row along the depressed aperture area.
Remarks: *Semitextularia thomasi* differs from *S. oscoliensis* in its significantly less indented outline and lack of peripheral spines.
Occurrence: widely recorded from the Middle Devonian of Siewierz (Racki and Soboń-Podgórska, 1993) and the Holy Cross Mountains at Wydryszów (Duszyńska, 1959; Fijałkowska-Mader and Malec, 2011), Skały (Duszyńska, 1956; Dubicka *et al*., 2021a,b; this study), Marzysz (Racki and Soboń-Podgórska, 1993), and Miłoszów (this study), the Middle Devonian of western New York (USA; Copeland and Kesling, 1955), the Middle Devonian of the Rhenish Massif, Germany (Sobat, 1966), the Middle Devonian of Moravia, Czech Republic (Pokorný, 1951), the Middle–Upper Devonian of the Russian Platform (Russia; Bykova, 1952, 1955), the Frasnian of the Voronezh Anteclise, Russia (Nazarova *et al*., 2019), the Frasnian of Alaska (Mamet and Plafker, 1982), the Upper Devonian of Iowa (Miller and Carmer, 1933; Cushman and Stainbrook, 1943), the Upper Devonian of northeastern Alberta, Canada (Loranger, 1954), and the Upper Devonian, Frasnian, of the Dinant Basin, Belgium (Mouravieff and Pultynck, 1966).

Semitextularia oscoliensis Bykova, 1952
Fig. 2H, I

1952 *Semitextularia oscoliensis* – Bykova, p. 33, pl. 8, figs 12, 13; pl. 9, figs 1, 2.

1965 *Semitextularia oscoliensis* Bykova – Chuvashov, pl. 14, fig. 12.

1993 *Semitextularia oscoliensis* Bykova – Racki and Soboń-Podgórska, p. 274, fig. 13a.

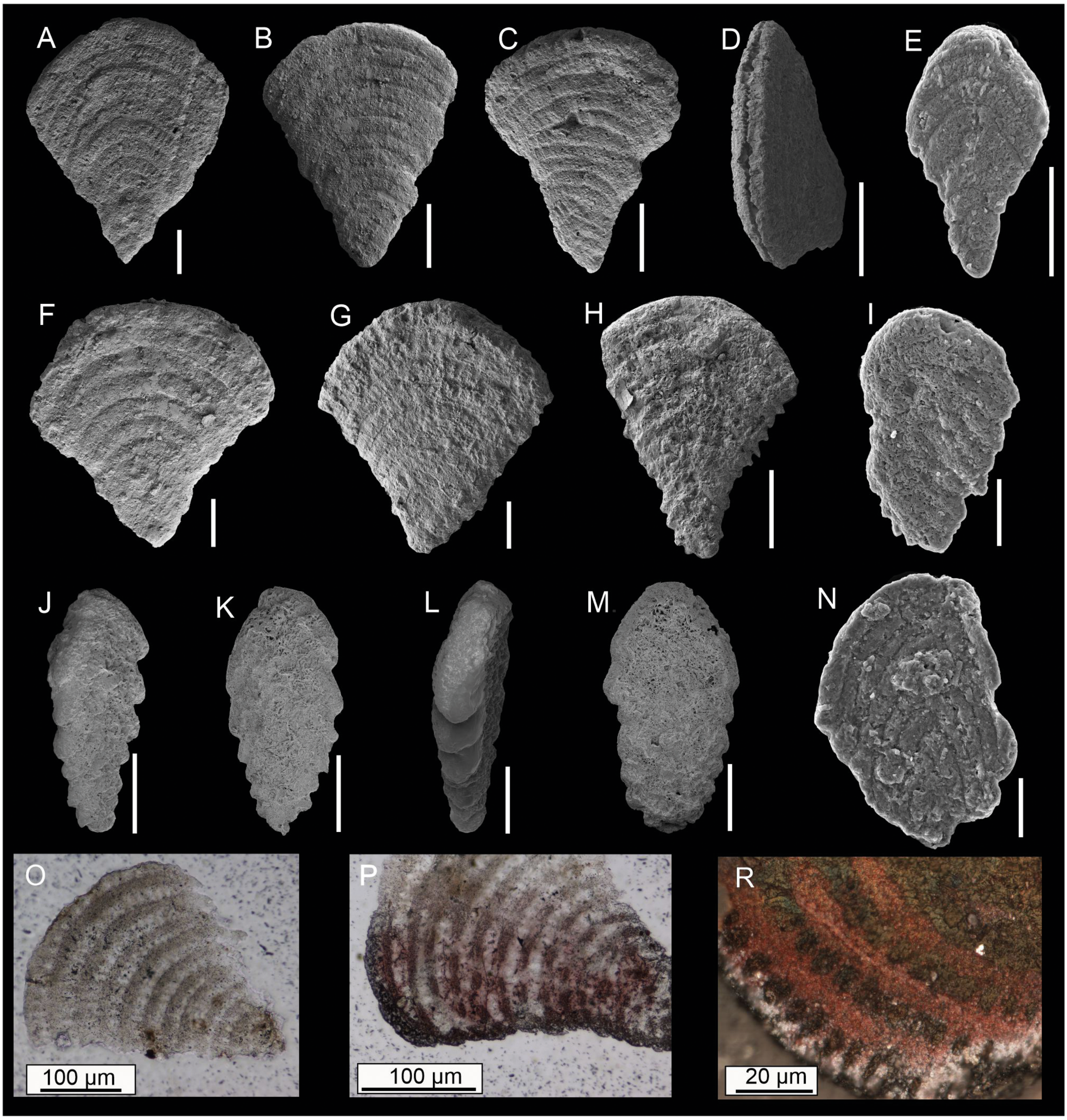

Fig. 2. Middle Devonian Foraminifera. **A–G, O–R.** *Semitextularia thomasi* Miller and Carmer (1933). A–G – SEM images of *Semitextularia* tests; A – Miłoszów, sample 12, MWGUW ZI/67/MG9.56; B – Miłoszów, sample 12, MWGUW ZI/67/MG9.14; C – Miłoszów, sample 12, MWGUW ZI/67/MG9.18; D – Miłoszów, sample O, MWGUW ZI/67/MG8.06; E – Miłoszów, sample 11, MWGUW ZI/67/ZD83SM13F; F – Miłoszów, sample 12, MWGUW ZI/67/MG9.14; G – Skały, sample 1, MWGUW ZI/67/MG9.53. O–R – internal test texture in a conventional-light microscope image showing transparent test. O – Miłoszów, sample 11, MWGUW ZI/67/MG03x20.01; P – Miłoszów, sample 12, MWGUW ZI/67/MG02x20.01; R – Miłoszów 12, MWGUW ZI/67/MG01x50.01. **H, I.** *Semitextularia oscoliensis* Bykova, 1952. H – Skały, sample A+11A, MWGUW ZI/67/MG6.26; I – Miłoszów, sample 12, MWGUW ZI/67/ZD83SM12. **J–M.** *Cremsia proboscidea* (Cushman and Stainbrook, 1943). J – Miłoszów, sample 11, MWGUW ZI/67/ZD73.11.01; K – Miłoszów, sample 11, MWGUW ZI/67/ZD73.12.01; L – Miłoszów, sample 11, MWGUWZI/67/ZD73.11.02; M – Miłoszów, sample 11, MWGUW ZI/67/ZD73.14.01. **N.** *Pseudopalmula palmuloides* Cushman and Stainbrook, 1943. Miłoszów, sample 12, MWGUW ZI/67/ZD83SM19. Scale bars A–N = 100 µm.

Material: Over 60 well-preserved isolated specimens

Description: The test is free, flattened on both sides, and fan-like in shape. The oldest chambers are semiovate, biserialy arranged, and rather poorly visible. They are followed by a series of narrow, variably U-arched, horizontally elongated and *uniserially arranged* (usually from 6 to 10). Test margins cover a row of characteristic irregularly shaped, peripheral spines – one per each chamber edge. Sutures between chambers are barely visible in the biserial part of the test but become much more clearly defined in the uniserial part. Test ornamentation visible on the test surface is a mesoporous structure with triangular pinholes. The thin section view shows a pattern of regularly chained chamberlets that are visible as round holes between rib-shaped pillars. The multiple apertures are created by small holes, arranged alongside the depressed area at the top of the last chamber.

Remarks: *S. oscoliensis* differs from *S. thomasi* by possessing peripheral spines at the test margins as well as by a slightly wider uniserial part of the test.

Occurrence: Scarce and recorded from the Eifelian and Givetian from Skały, Holy Cross Mountains, Poland (Racki and Soboń-Podgórska, 1993; this study) as well as Givetian of Russian Platform (Russia; Bykova, 1952)

Genus *Cremsia* Bykova, 1952

Cremsia proboscidea (Cushman and Stainbrook, 1943)

Fig. 2J–M

1943 *Textularia* (?) *proboscidea* – Cushman and Stainbrook, p. 78, pl. 13, fig. 32.

1952 *Cremsia proboscidea* (Cushman and Stainbrook) – Bykova, pp. 52–53, pl. 12, figs 12, 13; pl. 13, fig. 5.

1956 *Textularia* (?) *proboscidea* (Cushman and Stainbrook) – Duszyńska, 1956, pp. 30–32, pl. 11, figs 1–3.

1965 *Paratextularia proboscidea* (Cushman and Stainbrook) – Chuvashov, pl. 13, fig. 1.

Material: Few relatively well-preserved specimens

Description: The test is free, flatteed on both sides, and herringbone in shape. Chambers, usually from 12 to 14, are entirely biserialy arranged. The margin of the test is undulating because of the curved edges of protruding chambers. Characteristic ornamentation of mesoporous structure with triangular pinholes is visible on the surface of the calcareous walls. The sutures between chambers are rather wide and shallow. The aperture is terminal and located at the apex of the last chamber, unfortunately poorly represented in the studied material.

Remarks: very characteristic calcite test surface ornamentation, seen in both *Cremsia proboscidea* and *Semitextuaria* spp., indicates that representatives of both genera are calcareous and closely related therefore both are classified within the family Pseudotextularidae. However, *Cremsia* was variously designated in the literature as either agglutinated (*Textularia*) or calcareous (*Pseudopalmula)*.

Cushman and Stainbrook (1943) proposed assigning *Cremsia* to the genus *Textularia*, which was criticized by Duszyńska (1956), as it does not possess the coiling mode of the early chambers, typical for *Textularia*. Moreover, *Cremsia* does not display typical textularid features, such as the shape of the chambers. The ones of the studied form are not oval, nearly rounded, and short as in textularids, but elongated and narrower, visibly arranged in herringbone pattern, with one end of the chamber directed obliquely towards the proloculus.

Descriptions of the aperture in the previous works seem to be inconsistent. Cushman and Stainbrook (1943) recorded a single aperture, rounded in shape, sometimes located on the protruding short neck. Bykova (1952), who used the American textularids as the genotype for *Cremsia*, observed multiple apertures on a short neck. The occurrence of a neck is also recorded by Duszyńska (1965), although it is visible only in some specimens and the aperture is singular. The interpretation of a short neck was probably made on the basis of the visible protruding end of the last chamber that could imitate the occurrence of a neck. This could explain why it was not recorded in all the studied specimens. Specimens from Miłoszów and Skały do not show any neck remains at the top of the last chamber, but the state of preservation does not allow exclusion of the possible occurrence of multiple apertures, as was assigned by Bykova (1952).

Occurrence: Upper Eifelian and Givetian from Skały (Duszyńska, 1956; this study) and Miłoszów (this study) of the Holy Cross Mountains, Poland; Frasnian of Russia (Bykova, 1952) and Upper Devonian of North America (Cushman and Stainbrook, 1943).

Genus *Pseudopalmula* Cushman and Stainbrook, 1943

Pseudopalmula palmuloides Cushman and Stainbrook, 1943

Fig. 2N

1943 *Pseudopalmula palmuloides* – Cushman and Stainbrook, pp. 78–79, pl. 13, figs 35–57.

1952 *Pseudopalmula palmuloides* Cushman and Stainbrook – Bykova, p. 49, pl. 12, fig. 11; pl. 13, fig. 4.

1959 *Pseudopalmula palmuloides* Cushman and Stainbrook – Duszyńska, pp. 82–84, figs 5, 6.

Material: A single specimen.

Description: The test is wide, flattened on both sides, and entirely biserial. Chambers are rather narrow, elongated, and curved. The size and curvature of the chambers change sharply with growth. As a result, the younger chambers overlap the early ones as being significantly longer and more curved. Their ends are directed towards the spherical proloculus at the base of the test. Chambers are separated by distinct, slightly depressed, and narrow sutures.

Remarks: Cushman and Stainbrook (1943) recorded a nearly terminal and narrow aperture on the inner side of the end of the last chamber. However, it was not clearly visible on the collected specimen (this study) as well as on the specimens from Duszyńska's (1959) work.

Occurrence: Upper Emsian of Wydryszów (Duszyńska, 1959) and Givetian of Miłoszów of the Holy Cross Mountains, Poland (this study), Frasnian of Russia (Bykova, 1952), Upper Devonian of North America (Cushman and Stainbrook, 1943).

Family Moravamminidae Pokorný, 1951
Genus *Moravammina* Pokorný, 1951
Moravammina segmentata Pokorný, 1951
Fig. 3

1951 *Moravammina segmentata* – Pokorný, p. 7, fig. 7.

1955 *Moravammina segmentata* Pokorný – Bykova, pp. 25–26, pl. 6, figs 4, 5; pl. 8, figs 2, 5–11.

1956 *Moravammina segmentata* Pokorný – Duszyńska, pp. 24–25, pl. 2, figs 4, 5.

1965 *Moravammina segmentata* Pokorný – Chuvashov, p. 59, pl. 10, fig. 1.

1966 *Moravammina* sp. – Mouravieff and Bultynck, p. 154, pl. 1, fig. 11.

1993 *Moravammina* sp. – Racki and Soboń-Podgórska, p. 274, fig. 14.

Material: More than 100 specimens of different preservation.

Description: The test is of twofold composition: older parts are spirally coiled, while the younger part of the test becomes elongated and tubiform. The first chamber (proloculus) is spherical and large, sometimes of a similar size as the chambers from the uniserial part of the test. The number of coils is variable, usually from one up to three. The second part of the test becomes uniserial, elongated and uncoiled. The erect part is slightly winding, with chambers of irregular shape and size that increase only gradually, if at all. The wall is relatively thick, marked with distinctive narrow

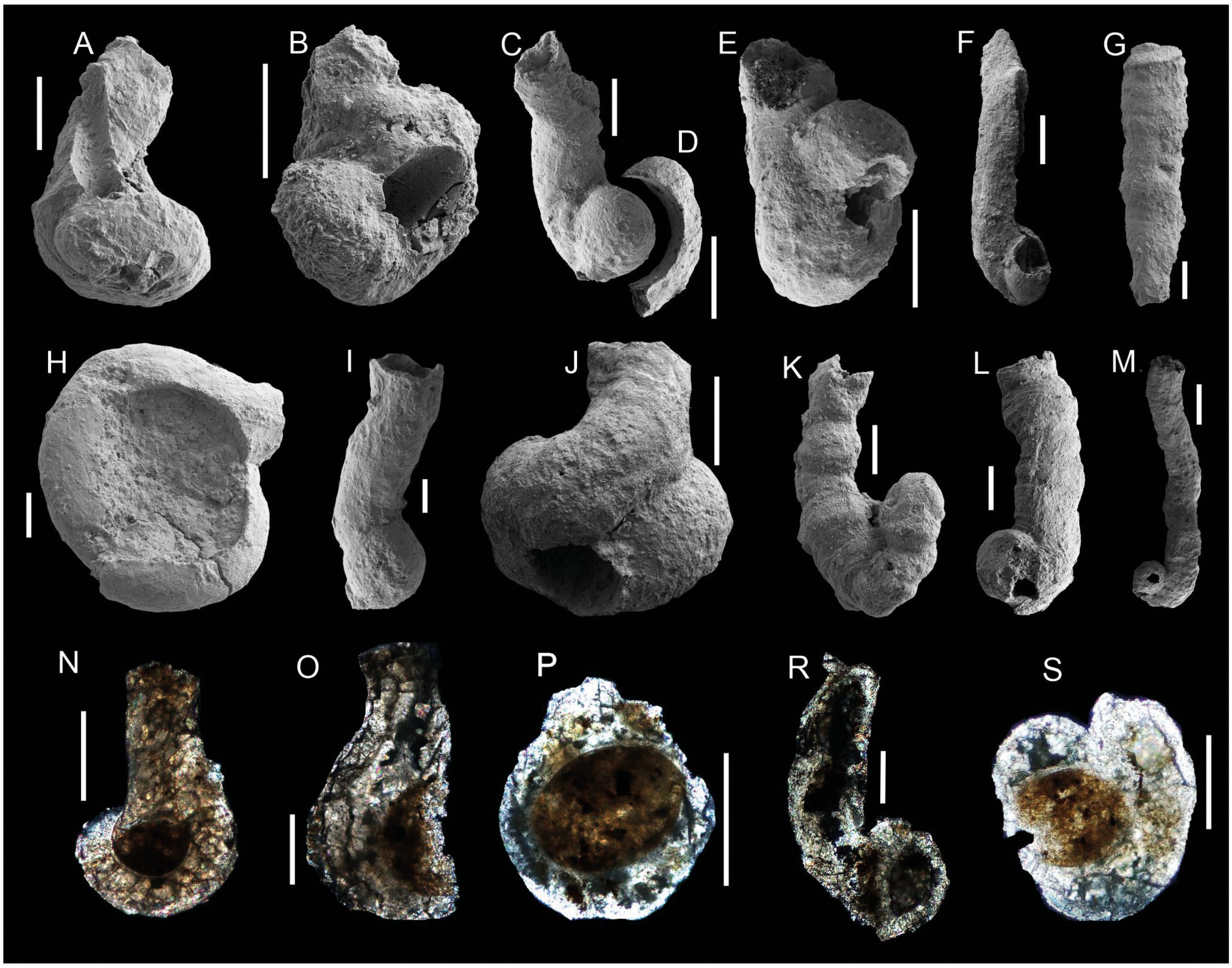

Fig. 3. Middle Devonian foraminifer *Moravammina segmentata* Pokorný, 1951. **A–M.** SEM images of the *Moravammina* tests; A – Miłoszów, sample 11, MWGUW ZI/67/MG10.55; B – Miłoszów, sample 11, MWGUW ZI/67/MG10.58; C – Miłoszów, sample 11, MWGUW ZI/67/MG10.56; D – Miłoszów, sample 4b, MWGUW ZI/67/MG10.43; E – Miłoszów, sample 1, MWGUW ZI/67/MG6.29; F – Miłoszów, sample 11, MWGUW ZI/67/MG5.17; G – Miłoszów, sample 11, MWGUW ZI/67/MG10.28; H – Miłoszów, sample 4c, MWGUW ZI/67/MG10.52; I – Miłoszów, sample 11, MWGUW ZI/67/MG10.60; J – Miłoszów, sample 11, MWGUW ZI/67/MG5.18; K – Miłoszów, sample 11, MWGUW ZI/67/MG10.57; L – Miłoszów, sample 12, MWGUW ZI/67/MG10.68; M – Miłoszów, sample 1, MWGUW ZI/67/MG6.28. **N–S.** internal test texture in a conventional-light microscope image showing transparent test; N – Skały, sample A+11A, MWGUW ZI/67/MGw.27; O – Skały, sample A+11A, MWGUW ZI/67/MGw.22; P – Skały, sample A+11A, MWGUW ZI/67/MGw.24; R – Miłoszów, sample 12, MWGUW ZI/67/MGw.35; S – Miłoszów, sample 12, MWGUW ZI/67/MGw.40. All scale bars = 100 µm.

sutures, and composed of calcite. Clearly marked septa subdivide the test perpendicularly to the axis of the tube. Most probably, the primary aperture is at the open end of the tube, but it is not preserved on any of the specimens.

Remarks: Chambers are coiled around a foreign particle, typically a grain, which is clearly visible in thin sections (fig. 2: 14–16, 18). Also, the tests show signs of being attached to elongated elements of the sea floor (fig. 2: 1, 2, 10), so they probably had a benthic sessile mode of life. Often the detached fragments of the coil (fig. 2: 4) are found independently in the residue, and the outline of a rounded first chamber is rarely visible.

Interestingly, a similar form was recorded by Miller and Carmer (1933) and by Cushman and Stainbrook (1943) from the Upper Devonian of Iowa, USA. Although morphological features of both *Lituotuba dubia* and the moravamminids studied herein show significant resemblances. Miller and Carmer stated that their form was agglutinated but their studies did not contain photos confirming this assumption. As a result, the relationship between these two forms cannot be excluded, but Pokorný (1951) noticed that the North American specimens in most cases did not show traces of attachment to the substrate and in some cases had differently oriented internal septa.

Occurrence: Eifelian and Givetian from Skały and Miłoszów of the Holy Cross Mountains, Poland (this study), Givetian of Čelechovice, Moravia, Czech Republic (Pokorný, 1951), Givetian and Frasnian of Kadzielnia, Sowie Górki, Siewierz, Poland (Duszyńska, 1965; Racki and Soboń-Podgórska, 1993), Frasnian of the Dinant Basin in Belgium (Mouravieff and Bultynck, 1966), Upper Devonian of the Middle and Southern Urals (Chuvashov, 1965).

Order Earlandiida (Vdovenko *et al.*, 1993)
Family Paratikhinellidae Loeblich and Tappan, 1984
Genus *Vasicekia* Pokorný, 1951
Vasicekia moravica Pokorný, 1951
Fig. 4A–F

1951 *Vasicekia moravica* – Pokorný, pp. 11–19, figs 8–12.

1965 *Vasicekia moravica* Pokorný – Chuvashov, pl. 14, fig. 1.

Material: More than 100 moderately well-preserved specimens.

Description: Tests are composed of a spherical, rounded first chamber (proloculus) and an erect, straight, or slightly curved tube of uniserially arranged chambers. The chambers are of elongated, cylindrical shape and rather similar in size. The wall is rather thick and unornamented. Sutures are distinctive but hardly visible in the poorly preserved specimens. Aperture is also hardly recognizable, as the ends of the tubes are open and seem to be mechanically damaged, however it appears to be located at the open end of the tube.

The proloculus usually ends with a circular serrate rim.

Remarks: There is an assumption that *Vasicekia moravica* could be closely related to the genus *Hyperammina*, as the specimens, documented by Cushman and Stainbrook (1943, p. 76, pl. 13, figs 14–17), show a great similarity of diagnostic features to those of *V. moravica.* It includes the occurrence of spherical to drop-shaped proloculus, from which extends a narrow tube. However, the comparison is restricted by the poorly detailed descriptions and low-quality photographic documentation of the *Hyperammina* specimens, but both taxa were found in sediments that are similar in age. However, the genus *Hyperammina* is characterized by an undivided tubular chamber and, most importantly, an agglutinated wall, which is not the case for the translucent and homogeneous tests of the *V. moravica* specimens.

Occurrence: Givetian of Moravia, Czech Republic (Pokorný, 1951); Middle Devonian from Miłoszów and Skały, Poland (this study).

Microfossils with uncertain biological position
Form A
Fig. 4BB–GG

1991 *Lagenosypho angustus* Langer, 1980 – Langer, p. 42, pl. 4, figs 7–9.

2002 *Incertae sedis 1* – Holcová, pp. 119–122, pl. 20, fig. 10.

Material: More than 60 poorly preserved specimens.

Description: The test is composed of an elongated single chamber with the more bulging, central part of the test. One end is more tapered, while the other is wider and broadens to a fan shape. The internal subdivision of the chamber is not visible. The wall is thin and unornamented.

Remarks: Langer (1979) identified such forms as bryozoan zooids that had a colonial mode of life.

Occurrence: Eifelian of Kačák Creek Valley, Czech Republic (Holcová, 2002), Givetian of Rhenish Slate Mountains, Germany (Langer, 1991), Middle Devonian strata of Miłoszów and Skały, Poland (this study).

Form B
Fig. 4HH–MM

1991 *Lagenosypho permianus* Spandel, 1989 – Langer, p. 42, pl. 4, fig. 3.

2002 *Incertae sedis 1* – Holcová, pp. 119–122, pl. 20, figs 9, 11, 12.

Material: More than 60 well-preserved specimens.

Description: A funnel-shaped and triangular form with a bulge at the central part of the test that widens significantly from the taper to the bulge. The apical part of the test ends with two tubes, located on the opposite sides of the terminal area. The first of them is erect, narrower, and longer than the other, which is much wider but usually preserved as a short neck. There is no evidence of a proloculus or internal division of the central chamber. The wall seems to be unornamented.

Remarks: Holcová (2002) suggests that the origin of these microfossils might be foraminiferal. However, their features indicate rather a bryozoan origin, as already was stated by Langer (1991). Probably the elongated, funnel-shaped tube of one specimen could have been attached to the second specimen with the long and narrow neck, located at the apical part of the test, allowing the colonial mode of life.

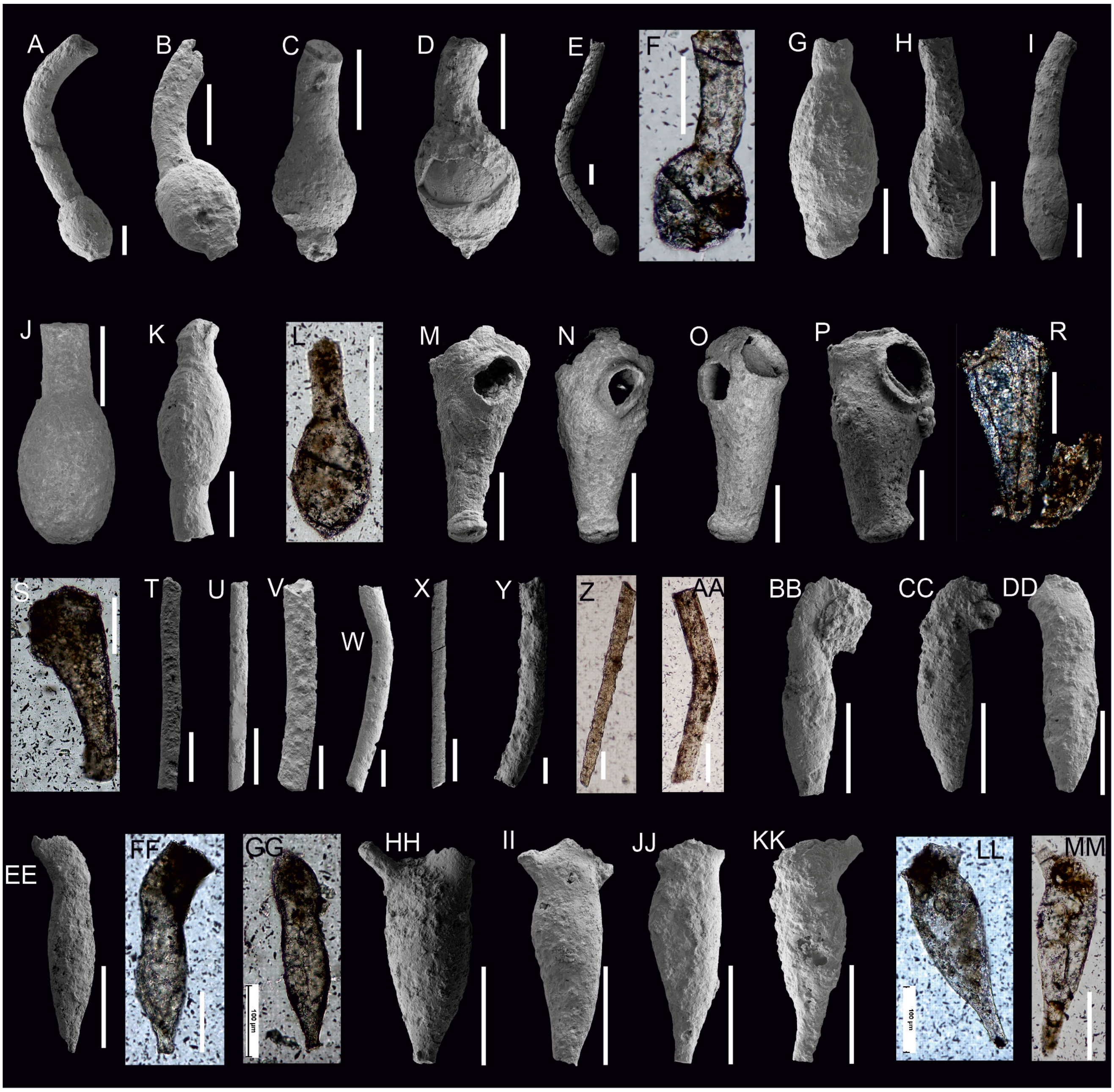

Fig. 4. Specimens of studied Middle Devonian foraminifer *Vasicekia moravica* and microfossils with the uncertain biological position. **A–F.** *Vasicekia moravica* Pokorný, 1951: A–E – SEM images of the foraminiferal tests; F – internal test texture in a conventional-light microscope image showing transparent test. **BB–GG.** Form A; BB–EE – SEM images of the microfossil tests; FF, GG – internal test texture. **HH–MM.** Form B; HH–KK – SEM images of the microfossil tests; LL, MM – internal test texture. **M–S.** Form C; M–P – SEM images of the microfossil tests; R, S – internal test texture. **T–AA.** Form D; T–Y – SEM images of the microfossil tests; Z, AA – internal test texture. **G–L.** Form E; G–K – SEM images of the microfossil tests. A – Miłoszów, sample 11, MWGUW ZI/67/MG10.54; B – Miłoszów, sample 2b, MWGUW ZI/67/MG10.27; C – Skały, sample A+11A, MWGUW ZI/67/MG6.25; D – Miłoszów, sample 4c, MWGUW ZI/67/MG10.13; E – Miłoszów, sample S, MWGUW ZI/67/MG5.34; F – Miłoszów, sample 4b, MWGUW ZI/67/MGk.100; G – Miłoszów, sample 4b, MWGUW ZI/67/MG10.50; H – Miłoszów, sample 4c, MWGUW ZI/67/MG10.08; I – Miłoszów, sample 1, MWGUW ZI/67/MG6.30; J – Miłoszów, sample 11, MWGUW ZI/67/MG10.25; K – Skały, sample 0, MWGUW ZI/67/MG10.35; L – Miłoszów, sample 12, MWGUW ZI/67/MGk.93; M – Miłoszów, sample 12, MWGUW ZI/67/MG10.70; N – Miłoszów, sample 12, MWGUW ZI/67/MG10.73; O – Miłoszów, sample 12, MWGUW ZI/67/MG10.72; P – Miłoszów, sample 12, MWGUW ZI/67/MG10.74; R – Miłoszów, sample 11, MWGUW ZI/67/MGb.45; S – Miłoszów, sample 11, MWGUW ZI/67/MGb.62; T – Miłoszów, sample 8a, MWGUW ZI/67/MG10.03; U – Miłoszów, sample 4b, MWGUW ZI/67/MG10.34; V – Miłoszów, sample 4c, MWGUW ZI/67/MG10.14; W – Miłoszów, sample 8a, MWGUW ZI/67/MG10.15; X – Miłoszów, sample 12, MWGUW ZI/67/MG10.75; Y – Miłoszów, sample 12, MWGUW ZI/67/MG10.76; Z – Miłoszów, sample 4b, MWGUW ZI/67/MGr.88; AA – Miłoszów, sample 4b, MWGUW ZI/67/MGr.89; BB – Miłoszów, sample 8a, MWGUW ZI/67/MG10.30; CC – Miłoszów, sample 8a, MWGUW ZI/67/MG10.01; DD – Miłoszów, sample 4c, MWGUW ZI/67/MG10.11; EE – Miłoszów, sample 4c, MWGUW ZI/67/MG10.09; FF – Miłoszów, sample 12, MWGUW ZI/67/MGb.58; GG – Miłoszów, sample 12, MWGUW ZI/67/MGb.64; HH – Miłoszów, sample 8a, MWGUW ZI/67/MG10.05; II – Miłoszów, sample 4c, MWGUW ZI/67/MG10.12; JJ – Miłoszów, sample 4b, MWGUW ZI/67/MG10.32; KK – Miłoszów, sample 11, MWGUW ZI/67/MG10.71; LL – Miłoszów, sample 12, MWGUW ZI/67/MGb.59; MM – Miłoszów, sample 12, MWGUW ZI/67/MGb.52. All scale bars = 100 μm.

Occurrence: Eifelian of Kačák Creek Valley, Czech Republic (Holcová, 2002), Eifelian and Givetian of Rhenish Slate Mountains, Germany (Langer, 1991), Middle Devonian strata of Miłoszów and Skały, Poland (this study).

Form C
Fig. 4M–S

Material: More than 150 well-preserved specimens.
Description: A chunky, funnel-shaped test with four openings in total. In the apical part, there are three large holes, in some cases ending with a short rim, that occupy even a quarter of the test surface. On the opposite side of the test, there is the last hole that evenly expands from a wide protruding rim. The rim is slightly wrinkled in some of the studied specimens. The wall is thick and unornamented. The interior of the central chamber is not divided, as seen in the thin-section view.
Remarks: This form is similar to form B in general outline and body plan, so most probably it is also a bryozoan. Both of them are characterized by a funnel-shaped test with openings on both ends. However, the main difference is that the apical holes of form B expand with a long neck, while in form C, the holes are larger and surrounded only by a short rim.
Occurrence: Middle Devonian strata of Miłoszów and Skały, Poland (this study).

Form D
Fig. 4T–AA

Material: Over 250 specimens.
Description: Thin, tube-shaped tests, straight or slightly curved. Both ends of the tube are open; a proloculus is not observed. Unornamented, thin walls of some of the specimens display internal septation. However, most of the tests do not show any subdivision into chambers.
Occurrence: Middle Devonian strata of Miłoszów and Skały, Poland (this study).
Remarks: The lack of clear diagnostic features of any group of microfossils, compounded by a rather a poor state of test preservation (most of them seem to be fragmentary) hinder proper biological identification of these microfossils.
Occurrence: Middle Devonian strata of Miłoszów and Skały, Poland (this study).

Form E
Fig. 4G–L

Material: More than 50 well-preserved specimens.
Description: Test free with a large ovate, rounded proloculus, and an elongated narrow and rather straight or slightly curved tube with an open end. The test surface is smooth with no ornamentation visible. Some specimens show two tubes extending from the proloculus but most of them have a circular serrated rim, instead of a second tube.
Remarks: This form has similar morphological features to *Vasicekia moravica* specimens. However, the proloculus of Form E is not spherical but more ovate and elongated. Moreover, in some specimens, two tubes extend from the proloculi in different directions. This indicates that probably more chambers could be bonded together by tubes into a chain. However, the author did not find any evidence, proving the colonial behaviour of the studied form.
Occurrence: Middle Devonian strata of Miłoszów and Skały, Poland (this study).

DISCUSSION

The origination of the first true calcareous, multichambered foraminifera is largely correlative with the development of the Devonian reefs (Vachard *et al.,* 2010; Vachard, 2016). Foraminifera have been recorded almost exclusively from shallow, warm reefal and lagoonal environments of the Devonian carbonate platforms (Vachard *et al.,* 2010) of North America (Miller and Carmer, 1933; Cushman and Stainbrook, 1943; Loranger, 1954; Copeland and Kesling, 1955; Kettenbrink and Toomey, 1975; Mamet and Plafker, 1982), Russia (Bykova, 1952; Timokhina and Rodina, 2015), the Czech Republic (Pokorný, 1951), Germany (Sobat, 1966) and Poland (Duszyńska, 1956, 1959; Racki and Soboń-Podgórska, 1993; Fijałkowska-Mader and Malec, 2011; this study, Fig. 5). The studied foraminiferal species are recorded from the Eifelian strata only from the Laurussian palaeocontinent (e.g., Duszyńska, 1956; Sobat, 1966; Mouravieff and Pultynck, 1966; unpublish data). The foraminifera found in the Givetian and Frasnian were also mainly from the area of Laurussia, but single Frasnian findings came from Gondwana (Vachard and Massa, 1989) and Siberia (Timokhina and Rodina, 2015). The most commonly found form was *Semitextularia thomasi*, numerously reported at first from the Holy Cross Mountains, Poland (Duszyńska, 1956; Dubicka *et al*., 2021b) and western Europe (Sobat, 1966; Mouravieff and Pultynck, 1966). Then, during the Middle Devonian, it spread from the European area to shallow Laurentian seas and shelves in the north- and southeast from the Rheic ocean basin. A similar distributional pattern can be seen for the *Pseudopalmula*, *Moravammina,* and *Cremsia* range extension as well.

During the Middle Devonian, foraminifera appeared to settle in various settings of *organic buildup* complexes from backreefs (lagoons) through fore-reef to off-reef environments (Vachard *et al*., 1994, 2010). Many foraminiferal occurrences were related to muddy-bottom sedimentary environments, in which marls and clay-rich sediments contain an abundant coral, stromatoporoid, and brachiopod shallow-water fossil fauna. In addition, *Semitextularia* was interpreted as inhabiting photic conditions that enabled foraminifer staying photosynthetically active by possession of symbiotic microalgae or plastids sequestered from ingested algae (Dubicka *et al.,* 2021b). However, this photic environment might vary in terms of the amount of penetrating light, as was suggested by the isotopic studies of the Skały and Miłoszów sections (Zapalski *et al.,* 2017; Dubicka *et al.,* 2021a).

Vachard *et al.* (2010) suggested that all Devonian foraminifers were probably endobenthic; however, moravamminids exhibited the features of a rather epibenthic habitat. Namely, the initial part of their tests shows clear traces of winding around an inorganic substrate or even parts of ramose organisms (Pokorný, 1951; Chovashow, 1987). In addition, semitextulariids, like their comparable modern

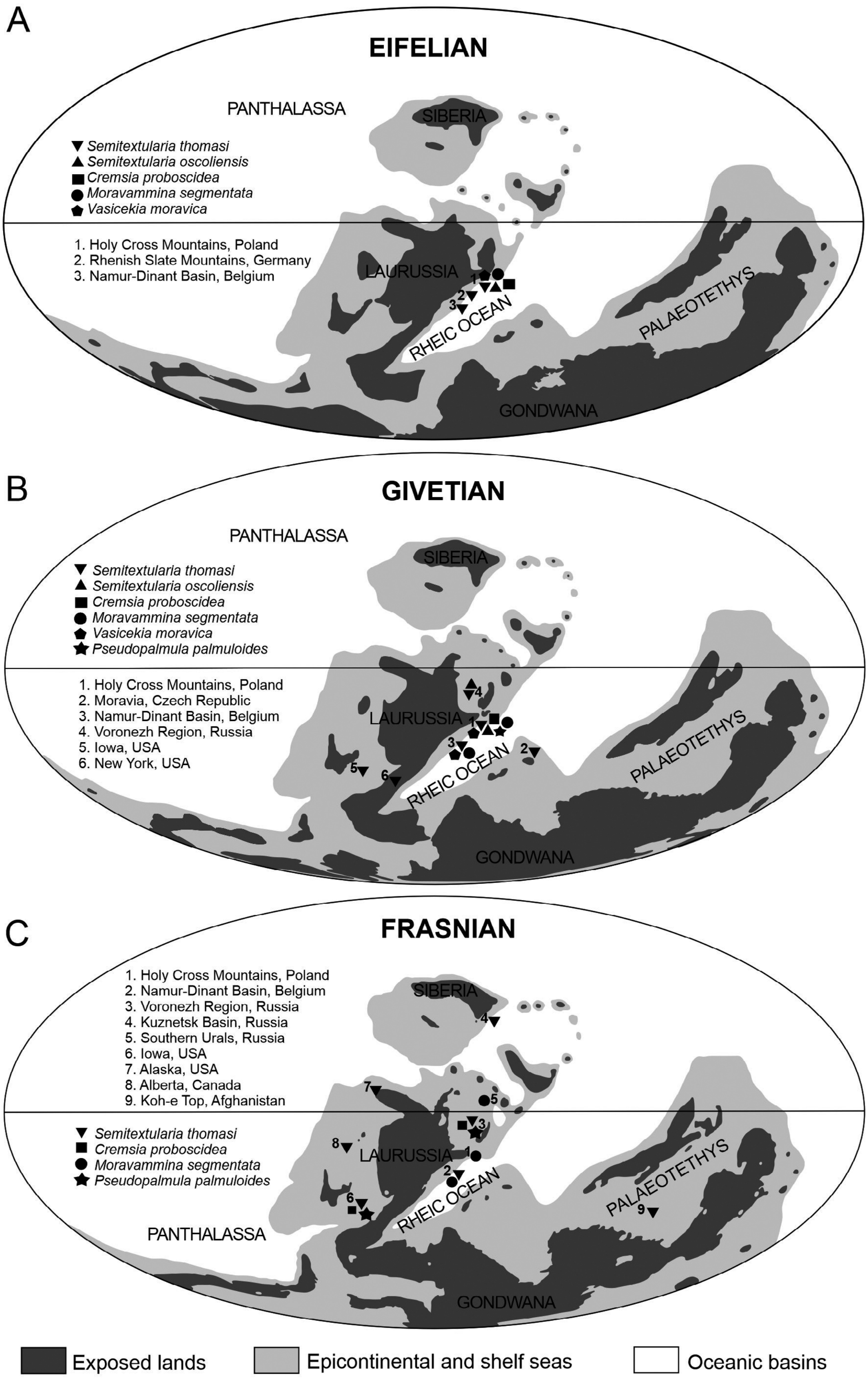

Fig. 5. Distribution of studied foraminifers in the Middle Devonian and Frasnian after Miller and Carmer (1933), Cushman and Stainbrook (1943), Pokorný (1951), Bykova (1952, 1955), Loranger (1954), Copeland and Kesling (1955), Duszyńska (1956, 1959), Mouravieff and Pultynck (1966), Sobat (1966), Kettenbrink and Toomey (1975), Mamet and Plafker (1982), Vachard and Massa (1989), Racki and Soboń-Podgórska (1993), Timokhina and Rodina (2015), Dubicka *et al.* (2021b), and studied data. Palaeomaps based on Scotese (2014).

morphological counterpart *Peneroplis*, were discussed by Dubicka *et al.* (2021b) as being epibenthic and possibly epiphytic foraminifera, which grew attached to algal filaments by pseudopodia that extended from multiple apertures (Dubicka *et al*., 2021b).

Miłoszów and Skały foraminiferal assemblages are abundant and diversified as at least six species, exceptionally well-preserved on a worldwide scale, are documented (*Cremsia proboscidea*, *Moravammina segmentata, Pseudopalmula palmuloides*, *Semitextularia oscoliensis*, *S. thomasi*, and *Vasicekia moravica*). Apart from the two-chambered *Vasicekia moravica*, the foraminifera show uni- or biserially arranged morphotypes. Calcareous serial foraminifera did not appear until the so-called 'Givetian revolution' – one of the greatest events in foraminiferal history, when the truly multilocular forms originated (Vachard *et al*., 2010).

The Foraminifera described from Miłoszów and Skały constitute a prime example of a typical Eifelian to lower Givetian assemblage with numerous palmate semitextulariids and uniserial moravamminids. There is still a lack of younger spiral *Nanicella* representatives which originated in the Givetian. Numerous nanicellids are known from the uppermost Givetian but primarily from the Frasnian strata of the Holy Cross Mountains (Racki and Soboń-Podgórska, 1993; Dubicka, 2017). Both the Miłoszów and Skały sections contain numerous specimens of *Semitextularia thomasi,* but only the samples from Skały contain *S. oscoliensis*, characterized by serrate wall margins. The co-occurrence of semitextulariids and nanicellids was, however, recorded from the Frasnian deposits of Afghanistan (Vachard and Massa, 1989), the Russian Voronezh region (Bykova, 1952), as well as the Kuznetsk Basin (Timokhina and Rodina, 2015). Many of the Devonian foraminiferal species, including palmate semitextulariids and spiral nanicellids, died out during the Frasnian-Fammenian biotic crisis, as these forms were strictly connected to the disappearing coral-stromatoporoid build-ups they inhabited (Vachard *et al*., 2010; Dubicka, 2017).

The richest of all Devonian foraminiferal assemblages so far recorded were described from Russia – about 50 species (Bykova, 1952), North America – 10 species (Cushman and Stainbrook, 1943, the Czech Republic – 8 species (Pokorný, 1951), as well as some Polish sites – 7 species (Duszyńska, 1959) and 15 species (Racki and Soboń-Podgórska, 1993). These faunas contained frequently recorded species of *Semitextularia*, *Pseudopalmula*, *Moravammina*, and *Nanicella*. The greatest similarity to the current assemblage in terms of species variability are the ones studied by Pokorný (1951) and Duszyńska (1959). However, these papers did not include detailed photographic documentation.

CONCLUSIONS

A detailed study of calcareous microfossils from the Devonian of Miłoszów and Skały reveals an abundant and diverse assemblage, containing (1) complex true multilocular foraminiferal species, belonging to the family Semitextulariidae Pokorný, 1956 (*Semitextularia thomasi* Miller and Carmer, 1933; *S. oscoliensis* Bykova, 1952; *Cremsia proboscidea* Cushman and Stainbrook, 1943 and a representative of *Pseudopalmula* Cushman and Stainbrook, 1943); (2) bilocular and tubular forms of the family Moravamminidae Pokorný, 1951 (*Moravammina segmentate* Pokorný, 1951; *Vasicekia moravica* Pokorný, 1951), and (3) foraminifer-like forms of uncertain affinities, representing at least six taxa (Forms A–E). Both the Miłoszów and Skały assemblages are of unique value, owing to their great variability and exceptional state of preservation, which provide new insights into the current knowledge of Middle Devonian foraminifera.

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